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DIETS OF SYMPATRIC RAPTORS IN SOUTHERN CHILE

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ABSTRACT.—We report on the diets of four sympatric raptor species in Torres del Paine National Park, Magallanes region, Chile. This assemblage includes some of the least-known raptors in southern South America. Two strigids, Great Horned Owl (*Bubo virginianus*) and Barn Owl (*Tyto alba*), had the most generalized diets. The Cinereous Harrier (*Circus cinereus*) preyed primarily on birds and lizards, and the Black-chested Buzzard Eagle (*Geranoaetus melanoleucus*) on the introduced European Hare (*Lepus capensis*). The Barn Owl and the Great Horned Owl, both nocturnal predators, preyed mainly on rodents and showed the largest dietary overlap. Raptor weight was positively correlated with mean weight of vertebrate prey but not with food-niche breadth.

Las dietas de aves rapaces simpatricas en el sur de Chile

EXTRACTO.—Se presentan las dietas de cuatro especies de aves rapaces en el Parque Nacional Torres del Paine, en la región de Magallanes, Chile. Este grupo incluye algunas de las especies de rapaces menos conocidas en el cono sur sudamericano. Dos estrigiformes, el Tucúquere (*Bubo virginianus*) y la Lechuza (*Tyto alba*), mostraron los hábitos alimentícios más generalizadas. El Vari (*Circus cinereus*) consumió principalmente aves y lagartijas, y el águila (*Geranoaetus melanoleucus*) predó principalmente sobre la liebre introducida (*Lepus capensis*). La Lechuza y el Tucúquere, ambos predadores nocturnos, consumieron principalmente roedores y mostraron los mayores índices de sobreposición de dieta. El peso de las aves estuvo positivamente corrélacionado con el peso promedio de la presas vertebradas, y no corrélacionado con el ancho del nicho dietético de las especies estudiadas.

The South American Patagonia steppe covers 565 000 km², with 465 000 km² in Argentina and the remainder in the southern portion of Chile. The Chilean Patagonia contains a highly diverse fauna (Miller and Rottmann 1976, Caviedes and Iriarte 1989), the result of a blend of faunas from the Chilean and Argentinean sides of the Andes. Eight falconiform and four strigiform species occur in the northern portion of the Chilean Patagonia (Johnson 1965, Venegas and Jory 1979, Araya and Millie 1986). Except for a brief report on Great Horned Owls (*Bubo virginianus*) (Jaksić et al. 1978) and Cinereous Harriers (*Circus cinereus*) (Jimenez and Jaksić 1988), no dietary information was previously

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available for raptorial birds from the Chilean Patagonia.

Here, we analyze the diets of an assemblage of four common raptor species in Torres del Paine National Park as they relate to prey availability. Specifically our objectives were to 1) determine the diets of two strigiforms, the Great Horned Owl and Barn Owl (*Tyto alba*), and one falconiform, the Black-chested Buzzard Eagle or Chilean Eagle (*Geranoaetus melanoleucus*), 2) compare our results with similar data on the Cinereous Harrier (Jiménez and Jaksić 1988), and 3) discuss these results in connection with prey distribution and current quantitative estimators of trophic structures (Jaksić 1985).

Study Area and Methods

Field studies were conducted in Torres del Paine National Park (51°3'S, 72°55'W) in the Magallanes region of Chile, on the eastern foothills of the Andes and on the western edge of Patagonia. Created in 1959, the 240 000-ha park provides relatively undisturbed habitat for wildlife. The topography of the study area ranges from foothills to plains with elevation ranging from 100–700 m. Approximately 80% of the park consists of steppe biome, classified as "pre-Andean, dry shrub association" and characterized by the pampa grassland common in both southern Chile and Argentina at elevations below 500 m (Pisano 1973, 1974). The remainder is a rich mosaic of lakes, shrub, and dense *Nothofagus* deciduous forest.

To analyze habitat use by prey species, we classified habitat as either grassland, shrubland, or *Nothofagus* forest. The most common grassland species in order of decreasing cover were *Festuca gracillina, Anarthrophyllum patagonicum,* and *F. palliscens* (Texera 1973, Pisano 1973, 1974, Ortega and Franklin 1988). The locally dominant shrubland species was "Mata Barrosa" (*Mulinum spinosum*), a spiny, dome-shaped shrub, common in thin, rocky upland and rapidly draining soils, and "Mata Negra" (*Verbena tridens*). Other important species were "Senecio" (*Senecio patagonicus*), "Calafate" (*Berberis buxifolia*), and "Paramela" (*Adesmia boronoides*). The *Nothofagus* forest habitats were dominated by two medium-size tree species, "Ñirre" (*N. antarctica*) and "Lenga" (*N. pumilio*).

Great Horned Owl pellets were collected beneath perches and nest sites of two pairs at the edge between open patches of grassland and *Nothofagus* forest near the park's administration office from January through March 1987 and from April through June 1988. Barn Owl pellets were collected at cliff nests of at least two pairs near Laguna Amarga, in the east part of the park from April through June 1988. Black-chested Buzzard Eagle pellets were collected beneath nine perches and five nests in *Nothofagus* forests in the northern portion of the park from April through June 1988.

We identified prey remains in pellets by comparing hair, feathers, and bones with our reference collection and with the key of Reise (1976). Mammalian prey was classified to the species level, with the exception of rodents of the genus *Akodon,* which we were unable to distinguish from prey remains. Avian prey were categorized to the family level.

We estimated habitat use and relative abundance of rodent species by trapping in the grassland, shrubland, and forest habitats from May 1987 through May 1988. Within each selected area we placed 49 (8 by 10 by 23 cm) Sherman aluminum live-traps in a 70 × 70 m grid with each trap 10 m apart. Traps were set each month for 4 days and 4 nights, baited with rolled oats, and checked daily in the morning. Additional trapping was conducted in areas not covered by the grids to determine the presence of species using more restricted habitats. Although we probably did not adequately sample certain trap-shy species and had to assume species had equal capture probabilities in each area, this index provided an initial measure of relative habitat use. We obtained raptors' weights from Jaksić et al. (1981), Jaksić and Delibes (1987), and Jiménez and Jaksić (1988). Food-niche breadth was determined using Levins' (1968) formula. This index ranges from 1 up to the number of prey categories recognized (n). We calculated food-niche breadth at the highest possible level of taxonomic resolution of prey categories, species level for mammals and family level for birds and insects.

To make comparisons among species that used different numbers of prey categories, we calculated a standardized food-niche breadth proposed by Colwell and Futuyma (1971:569). B_{sta} ranges between 0 and 1, or from minimum to maximum food-niche breadth.

Food-niche overlap, a measure of diet similarity, was calculated with the formula described by Pianka (1973). This index ranges from 0 (signifying no overlap) to 1 (signifying complete overlap).

Geometric mean weight of vertebrate prey in the diet was calculated by summing the products of the numbers of individual prey items with their natural-log weight and dividing by the total number of prey items used in the calculation. With the exception of species of the genus *Akodon* which we analyzed together, only prey items identified to species were included in this calculation. Average weights of prey were determined from adults of each species captured throughout the year. All prey were assumed to be adult-sized because we were unable to determine the frequency of occurrence of different prey sizes. This procedure overestimates the mean weight of prey for each raptor species, especially for the Black-chested Buzzard Eagle, which ate primarily European Hares, but the problem is partially alleviated by the use of natural-log-transformed weights to compute mean weight of vertebrate prey (see Jaksić and Braker 1983). Simple linear regression was used to determine the relation between mean weight of vertebrate prey, food-niche breadth, and raptor weight.

We used a chi-square analysis to compare the proportion of rodent species in the pellets and rodent abundance estimates to determine if the Barn Owl or Great Horned Owl preyed upon rodent species in proportions different than would be expected based upon the trapping results. Because of their low comparative abundances, *Reithrodon physodes, Auliscomys micropus, Euneomys chinchilloides, Phyllotis darwini, Eligmodontia typus,* and *Chelemys macronyx* were combined for statistical analysis (Sokal and Rohlf 1981).

Table 1. Diet of four raptors in Torres del Paine National Park, Chile, based on regurgitated pellets collected from January through March 1987 and April through June 1988 (subtotals in parentheses). Data on *Circus cinereus* were taken from Jiménez and Jaksić (1988).

	Barn Owl %	Great Horned Owl %	Chilean Eagle %	Cinereous Harrier %
Mammals				
Akodon sp.	30.1	22.2	—	—
Reithrodon physodes	19.6	9.3	—	—
Oryzomys longicaudatus	15.3	19.8	—	—
Auliscomys micropus	13.7	7.4	—	—
Eligmodontia typus	5.1	3.7	—	—
Phyllotis darwini	3.2	2.5	—	—
Chelemys macronyx	2.4	2.5	—	—
Euneomys chinchilloides	1.7	8.0	—	—
Unidentified rodents	8.7	3.1	2.1	28.9
Total rodents	(99.8)	(78.5)	(2.1)	(28.9)
Ovis aries	—	—	—	0.1
Lepus capensis	—	17.3	91.3	0.1
Dusicyon griseus	—	—	1.1	—
Conepatus humboldti	—	—	1.1	—
Unidentified mammals	—	—	1.1	—
Total mammals	(99.8)	(95.8)	(96.7)	(29.1)
Birds				
Anatidae	—	—	1.1	—
Emberizidae	—	—	—	0.6
Fringillidae	—	—	—	5.4
Furnariidae	—	—	—	1.5
Hirundinidae	—	—	—	0.1
Muscicapidae	—	—	—	0.1
Podicipedidae	—	—	—	0.1
Psittacidae	—	—	1.1	—
Tyrannidae	0.2	4.2	1.1	—
Unidentified birds	—	—	—	34.0
Total birds	(0.2)	(4.2)	(3.3)	(41.8)
Reptiles				
Iguanidae	—	—	—	29.1
Number of vertebrate prey	531	162	93	823[a]
Number of pellets	302	100	91	413
Food-niche breadth[b]	5.5 (0.5)	6.9 (0.6)	1.2 (0.3)	3.5 (0.3)
MWVP[c] (g)	29.9	80.3	2567.3	33.9
Raptor weight (g)	310	1500	2000	417

[a] Jiménez and Jaksić (1988) also found 436 remains of insects and arachnids in the pellets.
[b] Standardized food-niche breadth in parentheses.
[c] Mean weight of vertebrate prey.

RESULTS

Standardized food-niche breadth was broadest for Great Horned Owl, followed by the Barn Owl, Cinereous Harrier, and Black-chested Buzzard Eagle (Table 1). Dietary overlap was greatest between the Great Horned Owl and Barn Owl, because these two species preyed essentially on the same rodents (Table 2). The main difference between their diets

Table 2. Food-niche overlap among four common raptor species in Torres del Paine National Park, Chile.

	Great Horned Owl	Chilean Eagle	Cinereous Harrier
Barn Owl	0.818	0.051	0.496
Great Horned Owl	—	0.505	0.520
Chilean Eagle		—	0.309

was due to more European Hares in the diet of the Great Horned Owl and the comparatively larger percentage of *Akodon* spp., *R. physodes,* and *A. micropus* taken by the Barn Owl. The Black-chested Buzzard Eagle preyed primarily on European Hares (91% of its diet), whereas the Cinereous Harrier preyed mainly on birds (42%), lizards (29%), rodents (29%) and insects. Mean weight of prey in the diet increased with predator weight (Table 1), but not significantly ($r^2 = 0.60$, $F = 2.95$, df = 1, $P = 0.23$).

Three rodent species, *Akodon xanthorhinus, A. longipilis,* and *Oryzomys longicaudatus* accounted for 88% of the total trap captures. The majority of the rodents were captured in shrub and forest habitats (Table 3).

Neither owl preyed on rodent species in proportion to their availability (Barn Owl, $\chi^2 = 57.0$, df = 2, $P < 0.001$; Great Horned Owl, $\chi^2 = 55.7$, df = 2, $P < 0.001$), with both species selecting for the group of *R. physodes, A. micropus, E. chinchilloides, P. darwini, E. typus,* and *C. macronyx* and avoiding *Akodon* species.

The Barn Owl took a higher percentage of its prey from forested and shrub areas. *Akodon* spp., *O. longicaudatus,* and *A. micropus,* which together comprised 60% of the Barn Owl's diet, were trapped primarily in forested areas (Table 3). Similarly, the Great Horned Owl took rodents which we trapped mostly in shrub and forest habitats. Although this owl took some European Hares, inhabitants of open-patches (Grigera and Rappoport 1983), they preyed primarily on rodents trapped in dense cover such as *Akodon* sp., *E. chinchilloides,* and *O. longicaudatus.* The high proportion of European Hares in the Black-chested Buzzard Eagle diet indicated that this species hunted primarily in open habitats, which was the most extensive habitat in the park (more than 80% of the total study area).

Discussion

As previously reported for other areas of Chile (Johnson 1965, Jaksić and Yàñez 1979, 1980), we found that the Barn Owl in Torres del Paine National Park preyed primarily on rodent species. According to Jaksić et al. (1981), the Barn Owl in mediterranean-type habitats of central Chile preys

Table 3. Mean adult body weights and number of rodents captured per 1000 trap nights in the three most common habitat types in Torres del Paine National Park, Chile from May 1987 through May 1988.

	Mean Body Weight g (n)	Grassland	Shrub	Forest	Average
Akodon longipilis	31 (38)	0.4	100.7	130.5	77.2
Akodon olivaceus	27 (18)	1.7	58.0	31.3	30.3
Akodon sanborni	20 (4)	0.0	0.0	1.7	0.6
Akodon xanthorhinus	21 (49)	49.0	313.0	234.8	198.9
Auliscomys micropus	47 (5)	0.0	4.0	1.7	1.9
Chelemys macronyx	43 (3)	0.4	0.0	0.0	0.1
Eligmodontia typus	17 (3)	1.1	0.0	0.0	0.4
Euneomys chinchilloides	54 (2)	0.0	0.9	3.3	1.4
Oryzomys longicaudatus	26 (36)	0.4	127.5	102.6	76.8
Phyllotis darwini	52 (3)	0.0	0.0	3.3	1.1
Reithrodon physodes	60 (8)	1.1	23.3	8.8	11.1
Total captures		298	1424	1243	2956
No. trap-nights		5389	2275	2398	10 062
Captures/trap-nights		0.06	0.63	0.52	0.29
Number of species		7	7	9	11

on almost every small mammal species present. The degree to which the Barn Owl takes particular rodent species depends upon several factors. Apparent selectivity may result from differing degrees of nocturnal activity of the rodent prey, thus rendering some of them more readily available to this owl, a strictly nocturnal predator (Jaksić and Yàñez 1980). Foraging behavior and habitat use may also be important. The greater occurrence of *R. physodes* and *A. micropus* in the Barn Owl diet suggests they may be utilizing the shrub habitat more than the Great Horned Owl.

The prevalence of European Hares in the Great Horned Owl's diet compared to the Barn Owl parallels findings in central Chile (Jaksić and Yàñez 1979, 1980), where the latter species ate significant amounts of the European rabbit (*Oryctolagus cuniculus*). Our data showed that Great Horned Owls consumed a greater frequency of European Hare than previously reported for this species in the park (Jaksić et al. 1978, 1986). This apparent difference in diet can perhaps be attributed to seasonal or annual variations in prey availability, individual hunting behavior of owls, or even the use of a different habitat. According to Jaksić et al. (1986), in Chile, the geometric mean weight of prey consumed and diet breadth of the Great Horned Owl declined from north to south. Our results agreed with this general pattern as our consumed prey sizes and diet breadths are the smallest reported for Chile.

The Cinereous Harrier relied primarily on avian and small reptilian prey, taking some small mammals as well. This was the only raptor species in the study that ate reptiles and had a significant amount of insects in its diet (Jiménez and Jaksić 1988).

In our study the Black-chested Buzzard Eagle had the most restricted diet, feeding almost exclusively on European Hares. This raptor can be more of a generalist than our data suggests, however. For example, in central Chile, rodent species constituted 76% of the Black-chested Buzzard Eagles' diet (Schlatter et al. 1980). Also, since the European Hare was introduced in southern South America 90 years ago (Miller and Rottmann 1976, Grigera and Rappoport 1983), the Black-chested Buzzard Eagle has shifted its food habit considerably. Raptors are often considered to be opportunistic predators. The Black-chested Buzzard Eagle, being the largest aerial predator in the park, is likely to be the raptor best able to exploit the European Hare.

The presence of gray foxes (*Dusicyon griseus*) and of Patagonia hog-nosed skunks (*Conepatus humboldti*) in the diet of Black-chested Buzzard Eagles demonstrated their ability to take larger, and perhaps more difficult-to-catch prey, provided that they do not scavenge on carrion. The mean weight of vertebrate prey in the diet of Black-chested Buzzard Eagles in Torres del Paine was almost eight times that reported for central Chile (2367 vs. 308 g) (Schlatter et al. 1980). However, such large differences between different areas are not unusual among raptors (Jaksić and Braker 1983, Jaksić 1988).

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